

## Food reward in active compared to inactive men: Roles for gastric emptying and body fat

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**Title 1: Food reward in active compared to inactive men: Roles for gastric emptying and body fat**

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**Running Head:** Food Hedonics, Gastric Emptying, Activity

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## 29    **Abstract**

30    Habitual exercise could contribute to weight management by altering processes of food reward via  
31    the gut-brain axis. We investigated hedonic processes of food reward in active and inactive men and  
32    characterised relationships with gastric emptying and body fat. Forty-four men (Active: n=22;  
33    Inactive: n=22, BMI range 21-36 kg/m<sup>2</sup>; percent fat mass range 9-42%) were studied. Participants  
34    were provided with a standardised fixed breakfast and an ad libitum lunch meal 5h later. Explicit  
35    liking, implicit wanting and preference among high-fat, low-fat, sweet and savoury food items were  
36    assessed immediately post-breakfast (fed state) and again pre-lunch (hungry state) using the Leeds  
37    Food Preference Questionnaire. Gastric emptying was assessed by <sup>13</sup>C-octanoic acid breath test.  
38    Active individuals exhibited a lower liking for foods overall and a greater implicit wanting for low-  
39    fat savoury foods in the fed state, compared to inactive men. Differences in the fed state remained  
40    significant after adjusting for percent fat mass. Active men also had a greater increase in liking for  
41    savoury foods in the interval between breakfast and lunch. Faster gastric emptying was associated  
42    with liking for savoury foods and with an increase in liking for savoury foods in the postprandial  
43    interval. In contrast, greater implicit wanting for high-fat foods was associated with slower gastric  
44    emptying. These associations were independent of each other, activity status and body fat. In  
45    conclusion, active and inactive men differ in processes of food reward. The rate of gastric emptying  
46    may play a role in the association between physical activity status and food reward, via the gut-  
47    brain axis.

48    **Keywords:** liking; wanting; gastric emptying; physical activity.

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## 61 Introduction

62 Epidemiological studies consistently show that individuals who are physically active are less likely  
 63 to gain weight over time [1]. One hypothesis to explain why physical activity is crucial for weight  
 64 maintenance is that human physiology is biased towards maintaining energy balance at a high  
 65 energy flux (i.e. a high level of energy intake and energy expenditure) [2]. In support of this  
 66 hypothesis, in an early study of 213 workers with varying occupations in West Bengal (India),  
 67 Mayer [3] demonstrated that energy intake was more closely matched to energy expenditure in  
 68 physically active compared to sedentary workers. More recent evidence from both cross-sectional  
 69 and longitudinal studies further supports a role for physical activity in improved short-term appetite  
 70 control [4], [5], [6], [7], [8]. Blundell [9] termed the sedentary range ‘ the zone of dysregulation’  
 71 and proposed that people living in this zone are at a greater risk of overeating due to the lack of  
 72 physiological regulation that occurs within this range. The underlying mechanisms however remain  
 73 to be fully determined.

74 Day-to-day food intake involves the coordination of both non-homeostatic and homeostatic  
 75 signals, including psychological, physiological, behavioural and neural events [10] which interact  
 76 to form part of a ‘psychobiological system’ controlling appetite [11]. Food preferences and reward  
 77 pathways can exert a strong influence on food intake. Weight control can be enhanced or  
 78 undermined by the influence of exercise on hedonic processes of ‘liking’ and ‘wanting’ for food  
 79 which in turn alter food preference [12], [13]. For example, the impact of exercise on fat mass loss  
 80 has been shown to be diminished in some overweight and obese individuals who exhibit increased  
 81 explicit liking and wanting for food (particularly, high fat sweet foods) post-exercise [13].  
 82 However, whether food hedonics differ between habitually active versus inactive individuals has  
 83 not been examined.

84 Physiological signals arising from the gastrointestinal (GI) tract could also have a  
 85 mechanistic role in the influence of physical activity on appetite control [7], [14]. Gut peptides  
 86 released from the GI tract and gastric emptying (the rate at which food empties from the stomach)  
 87 play an important integrative relationship in the short-term control of food intake [15], and are  
 88 altered by physical activity level [16], [17]. We recently observed gastric emptying was faster in  
 89 habitually active compared to inactive men and was associated with activity energy expenditure  
 90 [17]. A growing body of work has demonstrated interactions between the food reward system and  
 91 signals from the GI tract [10], [18], [19], [20], [21]. Therefore, it is possible that signals from the GI  
 92 tract could interact with reward signals to influence food intake with habitual physical activity.

93 However, to the best of our knowledge, associations between hedonic processes of food reward and  
94 gastric emptying have not been previously investigated in humans.

95         Examining the relationships between gastrointestinal signalling and psychological processes  
96 involved in the control of food intake could improve the understanding of mechanisms involved in  
97 the impact of habitual physical activity on energy balance. In the current study, we aimed to 1)  
98 examine whether food preferences and implicit and explicit hedonic processes of ‘liking’ and  
99 ‘wanting’ differ between active and inactive men, and 2) determine whether gastric emptying  
100 predicts differences in food hedonics, with and without adjusting for body fat. As fat mass has been  
101 shown to correlate with eating behaviour and hedonic processes in overweight and obese  
102 individuals [22], [23], differences in body composition could be a confounding factor when  
103 comparing food reward between active and inactive individuals. Adjusting for body fat will allow  
104 effects of physical activity to be explored while controlling for fat mass.

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## 109 **Materials and Methods**

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### 111 **Design**

112 Participants in this between groups design study undertook two separate test mornings one week  
 113 apart: (1) body composition and energy expenditure assessment and 2) appetite behaviour/gastric  
 114 emptying assessment. Measures including body composition (assessed by air displacement  
 115 plethysmography), energy expenditure (activity energy expenditure assessed by accelerometry,  
 116 resting energy expenditure by indirect calorimetry) and gastric emptying (assessed by <sup>13</sup>C-octanoic  
 117 acid breath test) were taken as previously reported [17].

### 118 **Participants**

119 Forty-four men were studied. The sample size (n=22 Active and n=22 Inactive) was selected to  
 120 detect a minimum 10% difference between groups for the main GE outcome measure [24].  
 121 Inclusion criteria were: male, aged 18-55 yrs, BMI 18-40 kg/m<sup>2</sup>, weight stable (< ±4 kg change over  
 122 last 6 months), no history of GI surgery or disorder, non-diabetic, no medical conditions and not  
 123 taking medication known to influence gastric emptying or appetite, willing to consume study test  
 124 breakfast and lunch meals and not a heavy smoker (<10 per day). Participants were classified based  
 125 on their self-reported physical activity patterns over the last 6 months as either inactive (undertaking  
 126 ≤1 structured exercise session per week and not engaged in strenuous work) or active (undertaking  
 127 ≥4 structured exercise sessions per week). Individuals who did not fit either category were  
 128 excluded. One exercise session was defined as at least 40 minutes of moderate to high intensity  
 129 activity [4]. The study was conducted according to the guidelines laid down in the Declaration of  
 130 Helsinki and ethical approval was granted by Queensland University of Technology Research  
 131 Ethics Committee. All participants provided written informed consent.

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### 133 **Appetite Behaviour and Gastric Emptying Assessment Day Protocol**

134 Participants attended the laboratory after a 12-hour overnight fast, and having avoided alcohol and  
 135 strenuous exercise for 24 hours. Participants were provided with a fixed pancake breakfast labelled  
 136 with 100mg <sup>13</sup>C-octanoic acid (Cambridge Isotope Laboratories, Andover, USA), and spread with  
 137 butter and strawberry jam [1676 kJ (400 kcal); 15g (15%) PRO, 17g (37%) Fat, 48g (48%)  
 138 CHO)], and a 250ml drink of water. The test meal and drink were consumed within 10 minutes.  
 139 Gastric emptying of the meal was assessed by <sup>13</sup>C-Octanoic acid breath test as described [24].  
 140 Breath samples were collected in 10ml glass Exetainer tubes (Labco, Buckinghamshire, UK) prior

to the breakfast, immediately after, and subsequently every 15 minutes for 5 hours [24]. Data were analysed according to Ghooos et al. [25] as described [24] and the two main parameters lag time ( $t_{lag}$ ), reflecting the initial emptying rate, and half time ( $t_{1/2}$ ) were used in the present analyses. Participants remained in the laboratory in sedentary activities throughout the test morning. A lunch meal was served 5h after breakfast in the laboratory.

### **Subjective Appetite Sensations and Test Meal Palatability**

Subjective appetite sensations were measured immediately before and after breakfast, and periodically during the postprandial period using an electronic appetite rating system [26]. Participants were asked to rate feelings of hunger, fullness and desire to eat on 100 mm visual analogue scales, anchored at each end with the statements “not at all” and “extremely”. Five hour postprandial area under the curve (AUC) was calculated using the trapezoidal rule.

To assess palatability of the test meal, six questions concerning sweet, savoury, tasty, pleasant, filling and satisfying ratings were assessed on a 100mm scale using an identical electronic appetite rating system [26] immediately post consumption of the fixed breakfast meal.

### **Food Reward Assessment; Preferences, ‘Liking’ and ‘Wanting’**

Our operational definition of reward-value is through explicit liking and implicit wanting responses to high fat versus low fat and sweet versus savoury images of food. Food preferences and ‘liking’ and ‘wanting’ were examined immediately after breakfast consumption (fed state) which was repeated 5h later prior to lunch (hungry state) using a computer-based procedure - the Leeds Food Preference Questionnaire (LFPQ, for a detailed description see [27]). The LFPQ has been shown to demonstrate reliable immediate post-meal changes [27], is sensitive to changes in sensory specific satiation [28] and is a good predictor of food choice and intake in both laboratory and community settings [29], [30].

The LFPQ included 16 photographic food images administered using experiment software (E-prime v.1.2, Psychology Software Tools, ND). The foods were organised into separate categories of high fat savoury (HFSa), low fat savoury (LFSa), high fat sweet (HFSW) and low fat sweet (LFSW) (**Table 1**).

[Table 1 About Here]

171

172       Using the LFPQ, explicit ‘liking’ (the conscious feeling of pleasure expected from tasting  
173 each food [27]) was measured by presenting each food image one at a time on the computer screen  
174 and participants were asked to rate their perceived pleasantness of that food on a 100mm visual  
175 analogue scale, anchored at each end with ‘not at all’ and ‘extremely’. Mean ratings for each  
176 category were calculated. A higher score indicates a higher explicit ‘liking’ for that category.  
177 Implicit wanting was assessed according to each participant’s reaction time in selecting a type of  
178 food during each forced choice trial, adjusting for the frequency of selection and overall mean  
179 response time.

180       Preference for fat and sweet/savoury taste were evaluated by computing the fat bias (high fat  
181 > low fat) and the taste bias (sweet > savoury) scores for explicit liking and implicit wanting. The  
182 fat bias was calculated as the mean score for high fat foods minus the mean score for low fat foods.  
183 Thus a positive number indicates a high fat food bias and a negative number a low fat food bias.  
184 The taste bias was calculated as the mean score for sweet foods minus the mean score for savoury  
185 foods. Thus, a positive number indicates a sweet taste bias and a negative number a savoury taste  
186 bias.

187

## 188 **Statistical Analysis**

189 Data are expressed as mean  $\pm$  SEM unless otherwise stated. Differences between active and inactive  
190 groups were assessed by t test. To assess whether differences in percent fat mass (FM) contributed  
191 to these findings, the data were further analysed using ANCOVA, with percent FM as a covariate  
192 and activity status (active or inactive) as the independent factor. Changes from post-breakfast to  
193 pre-lunch were assessed by Repeated Measures ANOVA. Pearson correlation coefficients and  
194 multiple regression analyses were used to determine relationships between gastric emptying lag and  
195 half times, and process of food reward. To examine any influence of percent FM on the  
196 relationships observed, partial correlations were also undertaken controlling for percent FM.  
197 Statistical analysis was performed using PASW Statistics 18.0 (SPSS Inc., Chicago, IL) and Graph  
198 Pad Prism version 6.0 for Mac (GraphPad Software, San Diego, CA, USA). Statistical significance  
199 was set at  $P < 0.05$  unless otherwise stated.

200



Mean anthropometric, body composition, energy expenditure and physical activity characteristics were reported previously [17]. Key anthropometric, body composition and energy expenditure characteristics are summarised in **Table 2**. No participants were elite athletes. Gastric emptying was significantly faster in the active compared to inactive group (lag time ( $t_{lag}$ ): active:  $95 \pm 13$  and inactive:  $110 \pm 16$  min,  $P < 0.001$ ; half time ( $t_{1/2}$ ): active:  $157 \pm 18$  and inactive,  $179 \pm 21$  min,  $P < 0.001$ ).

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## 219 Comparison of Active and Inactive men in fed and hungry states

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231 Changes over time during the post prandial interval

232 As expected, ratings of liking and wanting assessed by the LFPQ changed over time during the test  
 233 morning from breakfast (i.e. fed state) to lunch 5h later (i.e. hungry state). Changes in explicit liking  
 234 for all foods and separate food categories from breakfast to lunch are shown in **Figure 1**. Active  
 235 men had a greater increase in explicit liking for all food categories combined (assessed by LFPQ)  
 236 between breakfast and lunch compared to inactive men ( $F(1, 42) = 4.13$ ,  $P = 0.048$ ), and  
 237 particularly for savoury foods (**Figure 1**). Trends in the differences observed between active and  
 238 inactive men remained after adjusting for percent FM (Liking All:  $P = 0.05$ ; Liking LFSA:  $P =$   
 239  $0.05$ ; Liking HFSA:  $P = 0.07$ ).

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241

242 [Figure 1 About Here]

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245 No significant differences in changes in implicit wanting over the postprandial interval were  
 246 observed between active and inactive men (**Table 4**).

247

## 248 Relationship of Food Reward Profiles with Gastric Emptying

249 Gastric emptying was negatively correlated with the increase in liking for LFSA foods ( $t_{1/2}$ :  $r = -0.34$ ,  
 250  $P = 0.02$ ) and increase in liking taste bias towards savoury foods ( $t_{lag}$ :  $r = -0.30$ ,  $P = 0.048$ ;  $t_{1/2}$ :  $r = -$   
 251  $0.30$ ,  $P = 0.045$ ) in the post prandial interval between breakfast and lunch. In addition, gastric  
 252 emptying was positively correlated with the liking taste bias for savoury foods when hungry ( $t_{lag}$ :  $r$   
 253  $= 0.48$ ,  $P < 0.01$ ;  $t_{1/2}$ : **Figure 2a**) and the average (average of fed and hungry states) liking taste bias  
 254 ( $t_{lag}$ :  $r = 0.44$ ,  $P < 0.01$ ;  $t_{1/2}$ :  $r = 0.36$ ,  $P = 0.02$ ). These correlations indicate faster gastric emptying  
 255 was associated with greater liking for savoury foods. Liking fat bias was not significantly correlated  
 256 with gastric emptying ( $P > 0.05$  for all).

Implicit wanting taste bias was not associated with gastric emptying ( $P > 0.05$  for all).

However, implicit wanting fat bias was positively correlated with gastric emptying when fed ( $t_{1/2}$ :  $r = 0.37$ ,  $P = 0.01$ ), and 5-hours later when hungry ( $t_{lag}$ :  $r = 0.31$ ,  $P = 0.04$ ;  $t_{1/2}$ : **Figure 2b**) and the average implicit wanting fat bias ( $t_{1/2}$ :  $r = 0.40$ ,  $P < 0.01$ ). These findings collectively indicate slower gastric emptying was associated with greater implicit wanting for high fat foods.

To examine any influence of body composition on the relationships observed, partial correlations were also undertaken. The significant correlations reported between food reward profiles and gastric emptying remained significant after controlling for body composition (BMI or percent FM) ( $P < 0.05$  for all).

[Figure 2 About Here]

Regression analysis revealed associations of gastric emptying  $t_{1/2}$  with liking taste bias and implicit wanting fat bias were independent of each other and activity status (gastric emptying  $t_{1/2}$  Model Adjusted  $R^2 = 0.37$ ,  $p < 0.01$ ; activity status  $\beta = 0.37$ ,  $P < 0.01$ ; liking taste bias  $\beta = 0.30$ ,  $P = 0.02$ ; wanting fat bias  $\beta = 0.28$ ,  $P = 0.03$ ). When BMI or percent FM were included in the same model, they did not contribute to any of the variance (BMI  $\beta = 0.01$ ,  $P = 0.99$ ; percent FM  $\beta = 0.00$ ,  $P = 0.99$ ) and the observed associations remained significant, indicating they were independent of body fat.

## 278 Discussion

279 This is the first study to compare measures of food reward and gastric emptying between active  
 280 versus inactive individuals. Our results demonstrate that food reward differs between active versus  
 281 inactive men and suggests that gastric emptying could have a mechanistic role in ‘liking’ and  
 282 ‘wanting’ processes of food reward.

283 Using a computer based assessment procedure, we observed that both explicit ‘liking’ and  
 284 implicit ‘wanting’ differed between active and inactive men. Firstly, active men displayed a lower  
 285 explicit liking for HFSA, LFSW and foods overall and showed a greater implicit wanting for LFSA  
 286 in the fed state, compared to inactive men. Elevated ‘liking’ and ‘wanting’ for energy dense foods  
 287 are considered psychological markers in individuals who are susceptible to overconsumption [31]  
 288 and involve both conscious (subjective, explicit) and subconscious (automatic, implicit) processes  
 289 [27], [32]. Indeed, one salient characteristic of individuals who binge eat appears to be the persistent  
 290 preference for sweet foods in the presence and absence of hunger, which has been demonstrated  
 291 under both laboratory and free-living conditions [33], using identical methodology as the present  
 292 study. Dalton et al. [34] reported that binge eaters had a greater explicit ‘liking’ for HFSW foods  
 293 and a greater implicit wanting for sweet foods in the fed state compared to non-binge eaters,  
 294 suggesting these characteristics may represent a marker for susceptibility to overeat. The hedonic  
 295 characteristics observed in binge-eaters are in contrast to the active individuals in our study. The  
 296 hedonic characteristics observed in the active individuals including lower liking for foods and a  
 297 greater implicit wanting for LFSA foods in the fed state could be one potential factor contributing to  
 298 improved appetite and body weight regulation that has previously been documented in more active  
 299 individuals [1], [3], [4], [6], [9].

300 We further observed that active men had a greater increase in ‘liking’ for all foods, in  
 301 particular savoury foods between breakfast (fed state) and lunch (hungry state - 5h after breakfast)  
 302 This is suggestive of a more sensitised appetite system in active compared to inactive men. ‘Liking’  
 303 for food has previously been shown to be greater when individuals are in a hungry (3-4 hours  
 304 postprandial) versus fed state [27], whereas this effect is reduced in individuals with higher binge  
 305 eating scores [35]. The greater increase in liking of savoury foods observed between the fed and  
 306 hungry states in active individuals may indicate that hedonic responses function more in response to  
 307 nutritional need-state in habitual exercisers compared to inactive individuals.

308 Interestingly, when compared to savoury foods, liking for sweet foods increased to a lesser  
 309 extent between the fed (post-breakfast) and hungry (pre-lunch) state and this was apparent in both  
 310 active and inactive men. It has previously been shown that ‘liking’ for sweet foods does not  
 311 increase to the same extent as fatty foods in hungry compared to fed conditions [27]. Moreover,

following a 24h fast, Cameron et al. [36] reported that ‘liking’ for savoury foods was greater in the hungry versus fed state, whereas ‘liking’ for sweet foods was unchanged. While historically, hedonic processes have been viewed as a function of nutritional need-state [27] - whereby in a state of depletion, the hedonic response (experienced palatability or pleasure) to foods is enhanced and when replete, the hedonic effect is reduced [37] - it is increasingly recognised that palatable sugar- and fat-rich foods can override satiation and promote overeating [38]. Hedonic responses to palatable sweet foods may therefore be less dependent on sensations of satiation and satiety than savoury foods. This may in part explain the blunted change in liking for sweet foods between the fed (post-breakfast) and hungry (pre-lunch) state that we and others [27], [36] have reported.

As could be expected, body composition differed significantly between active and inactive men and therefore could provide one plausible mechanism for the differences in food reward observed. Indeed, after adjusting for body fat, no significant differences in hedonic processes were observed in the hungry state between active and inactive groups, while in the fed state the higher liking for HFSA foods observed in inactive individuals no longer remained significant. This suggests that factors other than physical activity status, including body fat may contribute to hedonic processes in the hungry state and liking for high-fat foods in the fed state. Others have recently reported positive relationships between fat mass and wanting for high fat foods in particular, in overweight and obese individuals [22]. Nevertheless, the majority of differences observed between active and inactive men in the present study including liking for foods overall, liking for LFSW foods and implicit wanting for LFSA foods in the fed state, along with increases in liking for foods overall and LFSA foods in the postprandial interval, remained significant after adjusting for differences in body fat. These findings suggest physical activity status influences these hedonic processes, independent of body fat.

Differences in gut physiology could be one potential mechanism contributing to the differences in food reward we observed between active and inactive individuals in the present study. The inactive individuals had a slower gastric emptying and slower gastric emptying was associated with a higher fat mass as we recently reported [17]. A major aim of the present investigation was to examine potential associations between hedonic processes and gastric emptying. The phenomenon that information from the gut during a meal leads not only to decreased hunger and satiation but also to a feeling of reward is certainly not new [39], [40]. However, the signals and mechanisms involved remain to be fully elucidated. In our cross-sectional analyses of active and inactive men, we found that faster gastric emptying was associated with greater liking of savoury food whereas slower gastric emptying was associated with greater implicit wanting for high fat food. These relationships were independent of each other activity status and body fat and suggest that gastric emptying may have a mechanistic role in food reward. Our finding that faster gastric

emptying was associated with enhanced ‘explicit’ liking for savoury foods and with an increase in liking for savoury foods between the fed and hungry state is consistent with the view that hedonic responses to savoury foods may be associated with nutritional-need state i.e. the less food remaining in the stomach the greater the ‘liking’ for (savoury) foods.

Interestingly, in contrast to ‘liking’ for savoury foods and to this view, greater implicit ‘wanting’ for high fat foods was associated with slower gastric emptying. To the best of our knowledge relationships between ‘liking’ and ‘wanting’ and gastric emptying have not been previously documented in humans. However, Miras et al. [41] demonstrated that gastric bypass altered the reinforcing effects of sweet and fatty candy but not of vegetables, suggesting that gastric bypass results in the selective reduction of the reward value of a sweet/fat taste [42]. A reduced hedonic response and preference for high energy/fat foods has been increasingly documented in animal models and humans after gastric bypass [41], [43], [44] - a procedure which significantly accelerates the delivery of nutrients to the distal small intestine and alters gut hormone responses, but this has not been observed after gastric banding [43], [44] - a procedure which does not change the emptying rate or gut hormonal responses [15]. These alterations in gut physiology specific to gastric bypass may have a mechanistic role in the reduced hedonic response to high fat foods - findings which highlight the importance of the gut-brain axis in reward-based eating behaviour [43].

Our findings of a faster emptying rate being associated with a reduced implicit wanting for high fat foods are consistent with these observations after gastric bypass. One explanation may be that a slower gastric emptying would mean a reduced homeostatic drive and this could provide more opportunity for hedonic motivation to influence behavior, especially responses to high fat palatable foods. Additionally, the observed associations could be mediated by changes in gut hormones or dopamine release, both of which have been associated with the rate of gastric emptying [19], [45], [46], [47], [48], [49] and also linked to food reward [21]. The rate of gastric emptying plays an important role in the release of intestinal satiation peptides [49], [50], [51]. Moreover, in animals differences in gastric emptying rate are comparable to differences in dopamine efflux [45] and evidence suggests that stimulation of the GI tract with nutrients is sufficient to stimulate the release of dopamine in brain circuits controlling food intake [19]. A slower emptying rate could contribute to a blunted gut hormone or dopamine release and impairments in these pathways associated with food reward and control. As such the hedonic response to food could disrupt or override homeostatic signals of satiety.

The limitations of the present study should be considered. Given the cross-sectional nature of the study, causal relationships between gastric and hedonic responses are not possible to establish and this is an area that requires further investigation. Moreover, it is important to acknowledge that a wide range of genetic, environmental, psychological, and physiological factors contribute to the

short and long term control of food intake [52]. Gastric emptying and gut hormones have an integrative relationship in appetite control and gut hormones in turn may influence fatty acid detection or perception [44]. Characterising a combination of GI factors may therefore provide further mechanistic insight into differences in food reward with physical activity level. Furthermore, whether food reward differs between active and inactive men in response to other types of test meal as a result of sensory-specific satiety or if measured earlier in the postprandial period (e.g. at 3h) when hunger ratings are lower, is of interest. Findings may also be different in females and this is another area that requires further study.

In conclusion, these data demonstrate that in addition to differences in gastric emptying, habitual exercisers are characterised by different hedonic responses for high fat or low fat and sweet or savoury foods, compared to inactive individuals. These processes do not appear to operate independently. Interactions between the gut and hedonic aspects of appetite control could play a key role in the impact of habitual exercise on energy balance.

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## **Conflicts of Interest**

The authors have no conflicts of interest to disclose.

## **Authorship**

KMH, GF, NMB and NAK contributed to the design of the study; KMH collected the data, contributed to data analysis and drafted the manuscript; GF provided the experimental task, performed data and statistical analysis and contributed to critical revision of the manuscript. NMB and NAK provided critical revision of the manuscript. All authors read and approved the final manuscript.

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**Table 1.** Photographic food stimuli used in the food preference and 'liking' and 'wanting' computer task (grouped by food category)

HFSA	LFSA	HFSW	LFSW
Chips (fries)	Tomatoes	Doughnuts	Jelly beans
Pizza	Chicken	Chocolate	Juice
Meat pie	Rice	Milkshake	Mixed fruits
Swiss cheese	Boiled potatoes	Ice-cream	Apple

HFSA, high fat savoury; LFSA, low fat savoury; HFSW, high fat sweet; LFSW, low fat sweet.

**Table 2.** Participants' anthropometric, body composition and energy expenditure characteristics

	Inactive (n=22)		Active (n=22)		P-value
	Mean	SEM	Mean	SEM	
Age (years)	30.5	1.82	29.4	1.67	0.56
Height (m)	1.78	0.02	1.80	0.02	0.55
Weight (kg)	87.1	3.36	79.2	2.50	0.07
BMI (kg/m <sup>2</sup> )	27.4	0.89	24.5	0.55	<b>0.02</b>
Body Composition					
FM (%)	26.2	1.85	14.3	1.24	<b>&lt;0.001</b>
FFM (kg)	63.3	1.74	67.7	1.90	0.10
Activity EE (kcal/day) <sup>1</sup>	525	42	709	51	<b>&lt;0.01</b>
Total EE (kcal/day) <sup>1</sup>	2665	95	2890	92	0.09

Values are means ( $\pm$  SEM).

<sup>1</sup>Energy expenditure data refers to n=19 in Inactive group.

BMI, body mass index; FM, fat mass; FFM, fat free mass, EE, energy expenditure.

**Table 3.** Mean ( $\pm$ SEM) explicit liking and implicit wanting in fed (post-breakfast) and hungry (pre-lunch 5h later) states for different food categories in active (n = 22) compared to inactive (n = 22) men.

	Inactive (n = 22)	Active (n = 22)	Effect of Activity P-value (without adj.)	Main Effect %FM P-value	Effect of Activity after adjustment for %FM P-value
<b>Fed state</b>					
Liking HFSA	35.66 (4.65)	21.86 (4.05)	<b>0.03</b>	0.98	0.09
Liking HFSW	45.51 (4.64)	32.32 (5.03)	<b>0.06</b>	0.99	0.15

Liking LFSA	30.98 (4.05)	25.57 (4.42)	0.37	0.75	0.38
Liking LFSW	55.68 (3.65)	40.61 (4.37)	<b>0.01</b>	0.26	<b>&lt;0.01</b>
Liking All	41.96 (3.34)	30.10 (3.67)	<b>0.02</b>	0.67	<b>0.04</b>
Wanting HFSA	-7.14 (7.05)	-5.47 (7.04)	0.87	0.68	0.70
Wanting HFSW	10.03 (5.34)	-4.30 (7.86)	0.14	0.87	0.22
Wanting LFSA	-27.42 (5.88)	-5.61 (6.33)	<b>0.02</b>	0.35	<b>0.02</b>
Wanting LFSW	24.52 (6.49)	15.38 (6.33)	0.32	0.24	0.13

#### Hungry state

Liking HFSA	62.01 (4.14)	62.5 (4.93)	0.94	0.75	0.79
Liking HFSW	59.72 (4.08)	50.35 (6.42)	0.23	0.39	0.70
Liking LFSA	52.53 (3.65)	60.09 (4.11)	0.18	0.91	0.34
Liking LFSW	56.26 (3.54)	48.95 (3.67)	0.16	0.57	0.15
Liking All	57.63 (2.86)	55.47 (3.48)	0.63	0.78	0.75
Wanting HFSA	27.39 (6.00)	26.79 (7.17)	0.95	0.58	0.69
Wanting HFSW	-9.30 (5.14)	-21.18 (6.85)	0.17	0.19	0.82
Wanting LFSA	-4.06 (3.77)	12.24 (5.99)	<b>0.03</b>	0.51	0.19
Wanting LFSW	-14.03 (4.51)	-17.85 (5.15)	0.58	0.85	0.59

564 All, all categories of food combined; LFSA, low fat savoury; HFSA, high fat savoury, LFSW, low fat  
565 sweet; HFSW, high fat sweet.

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567 **Table 4.** Mean ( $\pm$ SEM) changes in explicit liking and implicit wanting for different  
568 food categories from fed (post-breakfast) to hungry (pre-lunch 5h later) states in  
569 active (n = 22) compared to inactive (n = 22) men.

	Inactive (n = 22)	Active (n = 22)	Effect of Activity P-value (without adj.)	Main Effect %FM P-value	Effect of Activity after adjustment for %FM P-value
<b>Change from fed to hungry state</b>					
Liking HFSA	26.35 (4.11)	40.64 (5.13)	<b>0.04</b>	0.73	0.07
Liking HFSW	14.22 (4.36)	18.00 (5.26)	0.58	0.33	0.30
Liking LFSA	21.56 (2.87)	34.52 (4.49)	<b>0.02</b>	0.81	<b>0.05</b>
Liking LFSW	0.58 (2.99)	8.34 (5.03)	0.19	0.56	0.17
Liking All	15.68 (2.58)	25.38 (4.02)	<b>0.05</b>	0.48	<b>0.05</b>
Wanting HFSA	34.53 (7.31)	32.27 (5.65)	0.81	0.31	0.41
Wanting HFSW	-19.33 (6.19)	-16.88 (5.18)	0.76	0.11	0.21
Wanting LFSA	23.36 (5.47)	17.85 (5.23)	0.47	0.09	0.10
Wanting LFSW	-38.56 (7.49)	-33.24 (6.15)	0.59	0.31	0.34

570 All, all categories of food combined; LFSA, low fat savoury; HFSA, high fat savoury, LFSW, low fat  
571 sweet; HFSW, high fat sweet.  
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## Figure Legends

Figure 1. Mean changes in explicit liking from breakfast to lunch (5h later) in active (n = 22) compared to inactive (n = 22) men, as assessed using the LFPQ. All, all categories of food combined; LFSA, low fat savoury; HFSA, high fat savoury, LFSW, low fat sweet; HFSW, high fat sweet. Error bars indicate SEM. \* p < 0.05.

Figure 2. (a) Scatter plot illustrating slower gastric emptying (i.e. longer gastric emptying  $t_{1/2}$ ) is associated with greater liking for sweet compared to savoury foods at pre-lunch. A positive taste bias score = liking for sweet foods > savoury foods. A negative taste bias score = liking for savoury foods > sweet foods. Partial correlations showed the relationship remained significant after adjusting for BMI (r = 0.43, P < 0.01) or percent FM (r = 0.38, P = 0.01). Removal of the extreme individual point for gastric emptying  $t_{1/2}$  (value: 231min) reduced r from 0.43 to r = 0.30, P = 0.04. (b) Scatter plot illustrating slower gastric emptying ( $t_{1/2}$ ) is associated with greater implicit wanting for high fat compared to low fat foods at pre-lunch. A positive fat bias score = wanting for high fat foods > low fat foods. A negative fat bias score = wanting for low fat foods > high fat foods. Partial correlations showed the relationship remained significant after adjusting for BMI (r = 0.37, P = 0.01) or percent FM (r = 0.32, P = 0.04). Removal of the extreme individual point for gastric emptying  $t_{1/2}$  (value: 231min) increased r from 0.36 to r = 0.43, P < 0.01. n = 44 for both.